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Design and management of linkage areas across headwater drainages to conserve biodiversity in forest ecosystems

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ABSTRACT

Biota in managed forest landscapes may be at risk from habitat fragmentation that prevents dispersal among subpopulations. Management provisions to provide connectivity are often considered independently for aquatic and terrestrial species. Of increasing concern is that dichotomous approaches are economically inefficient and may fragment populations that rely on both water and land. To provide habitat connectivity over ridgelines for such populations, which include many species of amphibians and arthropods, we propose designation of headwater "linkage areas." Essentially, we propose that headwater ridgelines be managed as important "linkage areas" to retain forested areas for species dispersal. Our process of linkage area planning, as demonstrated for headwater streams in the Coast Range of Oregon, USA, includes considerations at three spatial scales: landscape, drainage basin, and forest stand. At the landscape scale, linking headwater drainages across 7th-code hydrologic units (HUs) is a practical design regarding landscape connectivity for headwater species. In the Coast Range, each 7th-code HU adjoins an average of six 7th-code HUs. If each of these were linked via extending buffers or alternative forest management practices, about 5000 linkage areas would be provided in the 2.3-million ha landscape. We propose that the layout of such links considers site-to-landscape scale factors including known locations of target species, existing protections, land ownership patterns, dispersal capability of species of concern, climate change predictions, and the natural disturbance regime, such as landslide prone areas for managing wood and sediment inputs to streams. Although the proposed linkage areas target sensitive headwater species by design, the resulting web of connection across the landscape can be expected to benefit a host of forest-dependent species.

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1. Introduction

Retention of biodiversity in managed forest landscapes is an emerging issue worldwide (Brockerhoff et al., 2008; Olson, 2006). Biodiversity is a core component of forest ecosystem services at risk from anthropogenic disturbances (e.g., Millennium Ecosystem Assessment, 2005). Both species-based and habitat-based strategies have been proposed to conserve biodiversity in forests. A combination of approaches would likely best provide for long-term conservation of multi-species assemblages, including the rare and little known biota characteristic of most forests (Raphael and Molina, 2007; Lindenmayer et al., 2007; Lindenmayer and Franklin, 2002).

Management provisions are often considered independently for aquatic and terrestrial forest resources. Both types are commonly conserved through habitat-based approaches, with linear riparian reserves for aquatic biota and habitats, and upland block reserves or habitat element protections (e.g., structure-based management, dead wood provisions) for terrestrial resources. Of increasing concern is that such dichotomous approaches for aquatic and land systems are economically inefficient and may fragment populations and ecological processes that rely on both water and land. For example, many amphibians and arthropods have life histories dependent upon both aquatic and terrestrial habitats, and their movements between these habitats may provide reciprocal subsidies, such as transfer of nutrients between aquatic and terrestrial predator–prey networks (Baxter et al., 2005; Davic and Welsh, 2004; Olson et al., 2007). Similarly, hill-slope failures (landslides) may deliver sediment and wood to stream networks, which are important in providing habitat attributes for fish and other aquatic life forms (Reeves et al., 2003; Benda et al., 2003; Bigelow et al., 2007). Management designs that consider adjoining aquatic and terrestrial systems together are likely to sustain both species and ecological processes in a cost-effective manner and thus are useful to explore.

In the Pacific Northwest of North America, unique assemblages of amphibians and arthropods appear to be associated with forested headwater streams (Fig. 1) (Olson and Weaver, 2007; Rykken et al.,

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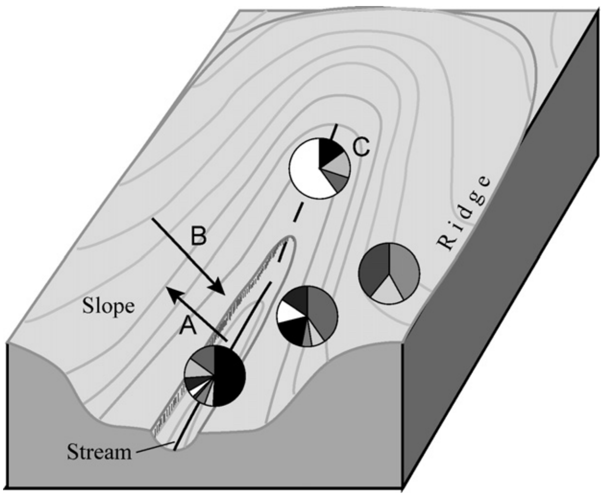

Fig. 1. Headwater drainages provide habitat for unique assemblages of biota, as depicted by pie charts reflecting differing species compositions. (A) and (B) arrows depict the "stream effect" gradient of cooler, moister microclimate conditions near streams to which both flora and fauna appear to respond. (C) A distinct assemblage associated with discontinuous streams in the uppermost headwater channel (Olson and Weaver, 2007). Linking areas over headwater ridgelines provide terrestrial connectivity for aquatic-riparian biota able to disperse overland.

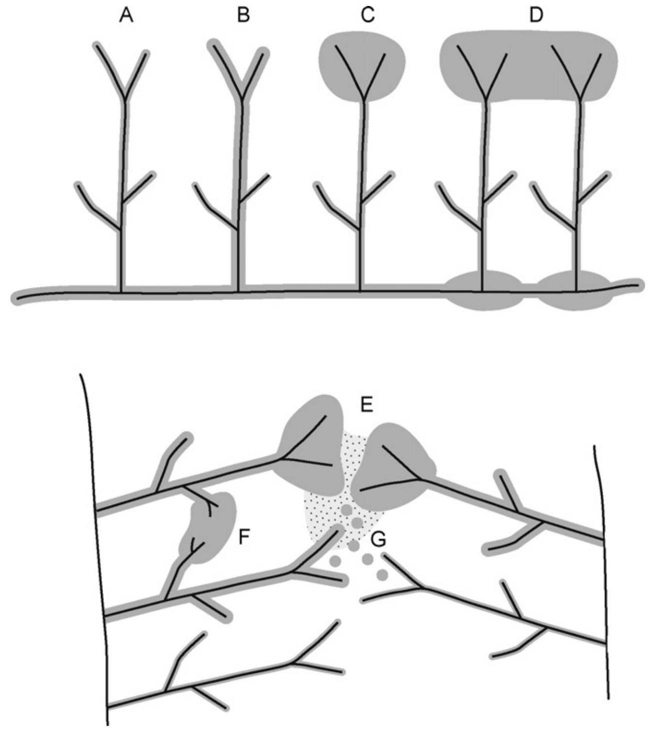

Fig. 2. Headwater management considerations to retain aquatic-riparian biodiversity by riparian buffers of different widths (A and B) and provide linkage areas between adjacent basins (C–G) using alternative forest management practices including uncut blocks (C, D, F), thinning (E) and leave islands (G) (figure from Olson et al., 2007).

2007; Sheridan and Olson, 2003; Progar and Moldenke, 2002; Wipfli and Gregovich, 2002). All forest-occurring amphibians in this region are obligate or facultative stream-riparian associates (Olson et al., 2007). Species highly associated with headwaters for certain functions (e.g., reproduction) may disperse over land, rather than through the stream network, during other life history stages; connectivity of forest habitat refugia across headwater ridgelines may be paramount for their successful dispersal (reviewed in Olson et al., 2007). For example, coastal tailed frogs (*Ascaphus truei*), endemic to the Pacific Northwest, are stream-breeders that appear to disperse more readily through intact upslope forests rather than clearcuts (Wahbe et al., 2004). This frog species is associated with headwater streams and is a species of concern relative to timber harvest practices (e.g., Welsh et al., 2005; Spear and Storfer, 2008); thus, it may benefit from headwater management for connectivity across ridgelines. Other terrestrial species also may be associated with strips of retained vegetation such as those along stream corridors. Either due to movements within those buffers or aversion to crossing water, such species may be channeled along stream-riparian buffers into headwaters and then disproportionately disperse overland between headwater drainages (e.g., ensatina, *Ensatina eschscholtzii*, western red-backed salamanders, *Plethodon vehiculum*; Olson and Weaver, 2007; Kluber et al., 2008). Many lentic-breeding amphibian and arthropod species also have the challenge of overland dispersal, and may similarly be associated with stream-riparian zones that essentially funnel them up to headwaters (e.g., rough-skinned newts, *Taricha granulosa*, and northwestern salamanders, *Ambystoma gracile*; Maxcy and Richardson, 2000; see also Olson and Weaver, 2007). Riparian buffers alone may not adequately provide for the terrestrial habitat connectivity needed by these diverse species assemblages in managed forests. Habitat links across ridgelines have been proposed (Olson et al., 2007). Such corridors offer incidental benefits for low-mobility terrestrial species as well, and likely those that are associated with contiguous intact vegetation conditions, including a host of rare or little known forest-dependent species (Raphael and Molina, 2007).

Although few studies specifically address corridor use by northwest forest amphibians, available data indicate some of these species do use corridors. The terrestrial salamander ensatina has been experimentally demonstrated to use forested corridors when there is high contrast to the surrounding managed land (Rosenberg et al., 1997). Moisture- and temperature-sensitive amphibians may detect microclimate gradients and remain in or disperse to corridors with lower temperatures and higher moisture contents. In British Columbia, more coastal tailed frogs (Wahbe et al., 2004), coastal giant salamanders (*Dicamptodon tenebrosus*, Johnston and Frid, 2002), and western red-backed salamanders (Dupuis, 1997) occurred along streams and in riparian corridors when upslope habitats were managed. These studies suggest that animal movements were restricted on lands managed for timber, increasing their use of riparian corridors (Olson et al., 2007).

Several approaches to forest management may provide forest habitats across headwater ridgelines to enhance connectivity relative to headwater- and riparian-occurring and forest-dependent species (Fig. 2) (Olson et al., 2007; see also Cissel et al., 1998). Essentially, we are proposing that headwater ridgelines can be managed to serve as important "linkage areas" to retain forested areas for species dispersal. Linkage areas are a current topic nationally in US state and federal wildlife management agencies, specifically for wildlife connectivity across expanses of non-habitat including high-disturbance areas such as paved road networks. Here, we further develop the conceptual framework for assessing: (1) how many linkage areas may be needed for forest-dependent biota across headwater drainages in forest landscapes; (2) where they might be located; and (3) what types of forest management, other than no-entry reserves, might be considered within linkage areas? We use the coastal forest landscape of Oregon, USA, and its resident biotic community, as our model system.

2. Methods and results

2.1. Quantity of headwater linkage areas: landscape scale

Headwater designs for habitat connectivity to retain biodiversity in managed forest landscapes must ultimately consider numerous questions. How much habitat is needed to conserve populations over broad areas? Is there a threshold level of connection for various species to provide gene flow across headwater ridgelines? If connectivity habitats are created, will biota be attracted to and differentially use these? How "swiss-cheesey" can the forest landscape become before species dispersal is impaired enough to affect population dynamics? Do species of interest have source-sink metapopulation dynamics, for example, such that if connections to source areas are severed then sink areas will eventually fail to support populations?

Although many questions related to habitat connectivity remain unanswered, conceptual recommendations for the quantity of connections have been proposed. These include: (1) "more is better" to facilitate dispersal and the use of corridors as habitat for other species' needs, and because more connections have been related to higher population densities in some circumstances (e.g., Steffan-Dewenter, 2003; Hilty and Merenlender, 2004); (2) establish higher densities of corridors when managing for species with poor dispersal capabilities (Lindenmayer and Franklin, 2002); (3) assess the relative degree of connectivity among alternative landscape designs because minimum standards are not available (Dobson et al., 1999); and (4) use the best science available including expert opinion and intuition because "corridor design is as much art as science" (Dobson et al., 1999). With these general guidelines in mind, we can proceed with alternative management scenarios to address the headwater linkage issue.

We develop and evaluate a landscape design based on hydrologic units to address headwater linkage areas in the Oregon Coast Range Physiographic Province (Fig. 3A). This Province covers approximately 23,000 km^2 of forests that are primarily within the western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness, 1988), with Douglas-fir (*Pseudotsuga menziesii*) as the dominant overstory tree. It is part of an ecoregion that extends from southern Oregon into British Columbia, Canada. Lands are in a mix of federal, state, and private ownerships managed primarily for forested uses but under widely different forest policies (Spies et al., 2007). Hydrologic units were selected because the amphibian species we target in headwaters are stream-breeders, and the basis of our management approach is to extend existing riparian corridors to connect headwater riparian areas in neighboring sub-drainages over ridgelines. Additionally, land-use planners in the Pacific Northwest have experience working with landscape designs based on drainage units due to fisheries management issues.

We used the hydrologic unit (HU) code system (for more information: http://water.usgs.gov/GIS/huc.html) for analysis, which delineates nested units by drainage area within the larger study area. Larger HU code numbers designate smaller areas. The study area consists of 17 "4th-code hydrologic units" (4th-code HUs). One of these is the Siuslaw River basin (2000 km^2) (Fig. 3B), which contains 48 6th-code HUs (mean area = 69 km^2), and 109 7th-code HUs (mean area = 14 km^2) (Fig. 3C). The 7th-code HUs encompass numerous first-order (Strahler, 1957) headwater tributaries that extend toward ridgelines. These small tributaries may include perennially flowing streams, spatially intermittent (discontinuous) streams, and temporally intermittent (ephemeral) streams.

The 7th-code HU was chosen as the scale of reference to aid headwater species dispersal because it was both "small enough" and "large enough." Seventh-code HUs are small enough to consider for the practical movements of individuals across ridgelines, yet are large enough to represent likely subpopulations of animals that may have dispersal limitations downstream along aquatic networks. Downstream considerations include increasing stream size and increasing likelihood of instream predators, such as salmonid fishes and larger life history stages of giant salamanders (e.g., Rundio and Olson, 2001, 2003).

On average, each 7th-code HU adjoins six neighboring 7th-code HUs in the Siuslaw River basin. Hence, if linkage areas were to be designated across adjoining HUs, this yields an average of six links per 7th-code HU. In the Siuslaw River basin, this design of overland connectivity results in 376 linkage areas or one link per 5.3 km^2 (Fig. 4). If this linkage criterion was replicated across the Oregon Coast Range Province, an estimate of over 5000 linkage areas would be created. This exceeds one link per 4.6 km^2 (5000 links/23,000 km^2).

To assess how much connectivity this implies, we estimated the proportion of headwater tributaries that would be connected by this design. In the Siuslaw River basin, we took a representative subsample of ten 7th-code HUs and counted the number of headwater tributaries in those HUs. A headwater tributary was included in the count if it met two criteria: (1) it extended toward a ridgeline, eventually ended in flow, and was a candidate for over-ridge linkage (e.g., in Fig. 2, see tributaries E and G for potential linkage across distinct basins) and (2) it had a 95% probability of perennial flow, based on a cumulative distribution function constructed from drainage areas corresponding to the upper limit of field-determined perennial flow for streams in the Oregon Coast Range Province (Clarke et al., 2008). Hence, we did not count dry or largely ephemeral channels. The number of tributaries averaged 39.5 (range: 21–69) for the ten 7th-code HUs we sampled. With each 7th-code HU adjoining an average of six neighboring 7th-code HUs, we roughly estimated that six of 39.5 (15%) of the headwater streams would be connected by this design. Per 7th-code HU, the level of connectivity would be greater for smaller HUs with more HU neighbors, and for some stream network configurations. For example, the tributary counts were smaller and less variable for 7th-code HUs that are true watersheds containing only small headwater streams (mean tributary count = 32.6; SD = 7.7; N = 5; connectivity = 6/32.6 or 18.4%) than for 7th-code HUs that are composite watersheds (i.e., contain two or more streams that do not drain to a single point or may have channelized flow into the unit [Omernik, 2003]) (mean tributary count = 46.4; SD = 17.1; N = 5; connectivity = 6/46.4 or 13%). Application of a rate of connectivity per HU (e.g., 15%) rather than a number (e.g., six links per HU) would allow more consistent levels across the landscape. Application of a range of rates (10–20%) would allow even greater management flexibility to consider a variety of factors in landscape design, and could allow natural resource managers to focus on conservation or timber production priorities in designated areas.

If this level of connectivity was deemed insufficient to retain life history functions and thriving populations across the forested landscape, additional linkage areas per 7th-code HU could be considered. In contrast, if this level of connectivity was judged excessive, fewer linkage areas might be considered. For example, the same approach could be used with 6th-code HUs as the unit for connectivity. Each 6th-code HU in the Siuslaw River basin adjoins an average of six neighboring 6th-code HUs. Hence, if these were to be linked across the Oregon Coast Range Province in the same manner as described above, roughly half the connectivity would result, or approximately 2500 linkage areas, one link about every 9.3 km^2.

Due to the hundreds of rare or little known species and species with low dispersal capabilities in this forested zone (Raphael and Molina, 2007), we recommend a more-connected rather than a less-connected landscape, resulting with links based on the 7th-code or higher level HU criterion. Once additional knowledge of species dispersal capabilities and rates is available (Johnston and Frid, 2002; Curtis and Taylor, 2003), the number of linkage areas could be refined. Additional

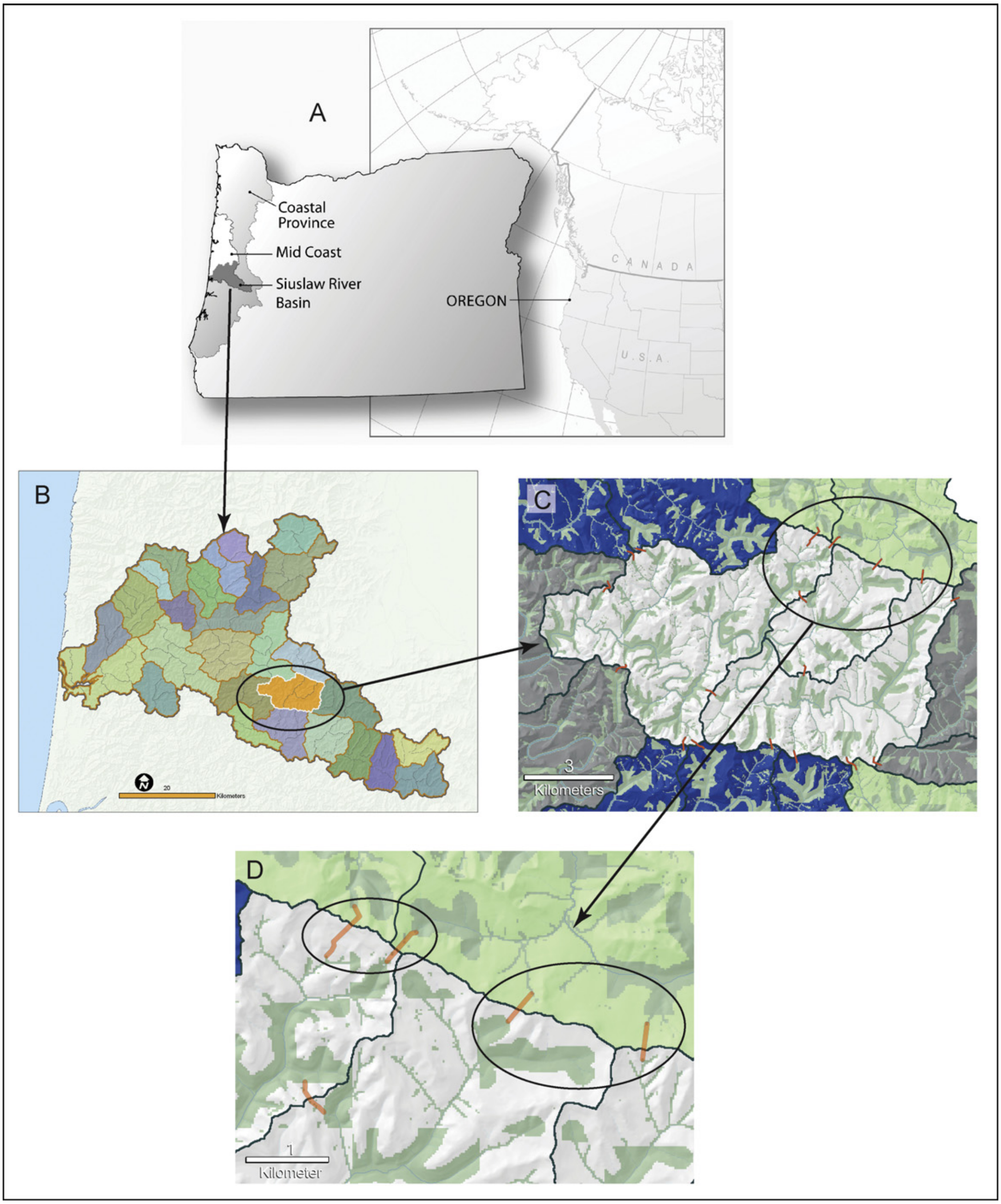

Fig. 3. Linkage areas between hydrologic units at different spatial scales in the (A) Siuslaw River basin of the Oregon Coast Range Physiographic Province, USA, showing (B) nesting of 5th-code hydrologic units (HUs) within the 4th-code hydrologic units (HUs) of the Siuslaw River basin, and (C) linkage areas providing connectivity of headwater habitats across a landscape at the scale of 6th-code HUs and (D) 7th-code HUs. This illustrates a design of one link between adjacent 7th-code HUs (orange line).

considerations at the landscape scale for determination of linkage area densities include the following.

2.1.1. Connections across larger basins

River basins with no freshwater connectivity would need higher densities of linkage areas because there is no chance of incidental dispersal along downstream connected riparian corridors. Hence, we propose higher densities of linkage areas across ridgelines of 4th- and 5th-code HUs than across ridgelines between 6th-code HUs that are contained entirely within a single 5th-code HU. In the example of the Siuslaw River basin, a 4th-code HU, there are 116 linkage areas around the periphery of the watershed to other 4th-code HUs, which is 31% (116/376) of the 7th-code links identified for the entire basin (Fig. 4). Weighted protection of these peripheral linkage areas would aid between-basin dispersal, and retain connected populations across natural aquatic boundaries at the landscape scale.

2.1.2. North-south migration corridors

Protection of north-south dispersal routes is proposed to enhance species migratory options in the face of climate change scenarios (e.g., Primak, 2006). Generally, this argument follows from patterns of change in climate conditions along latitudinal gradients, with latitudinal connectivity permitting movements that enable organisms to survive variable or altered conditions in one part of their range, or to move to new areas that become

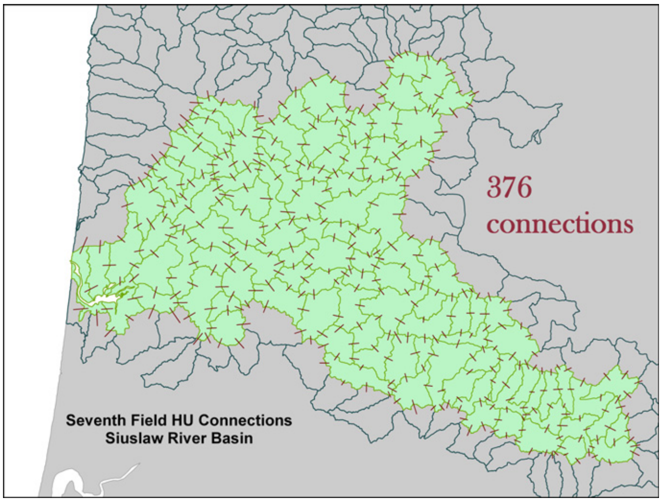

Fig. 4. Headwater linkage areas illustrated for the Siuslaw River basin in Oregon, USA. A single connection between adjacent 7th-code hydrologic units (HUs) results in 376 connections across the basin. This approach would produce ~5000 linkage areas within the 23,000 km^2 area of the Oregon Coast Range Physiographic Province, which is estimated to protect about 15% of headwater tributaries.

hospitable. Hence, prioritized retention might be considered for linkage areas at the northern and southern boundaries of 4th- or 5th-code HUs. This argument could also be applied to altitudinal gradients, if organisms are predicted to move into higher elevations in response to climate change, or to other environmental gradients such as across ecoregion boundaries.

2.1.3. Linking landscape fragments

Increased connectivity might be considered among landscape fragments of older forests, to promote movements of numerous species associated with these areas, including dispersal-limited organisms such as mollusks, lichens and bryophytes. Similarly, if a reserve system has been previously designed that resulted in an archipelago of discrete patch reserves, connection of these patches via riparian corridors and ridgeline linkage areas could be considered.

2.1.4. Landscape-scale disturbance patterns

Fewer linkage areas would need to be identified in sections of landscapes subject to less disturbance, including areas with less timber harvest (Lindenmayer and Franklin, 2002). Conversely, it follows that more linkage areas would need to be considered in parts of landscapes with higher disturbance, including higher frequency or intensity of species' habitat alteration from forest management activities. Both anthropogenic and natural disturbances are discussed further at the smaller spatial scale of drainage-basins.

2.2. Location of headwater linkage areas: drainage-basin scale

At the scale of 6th- or 7th-code HUs, or the operational scale of land-use planning such as timber harvest units, trade-offs between biodiversity conservation and the economics of a managed forest landscape will need to be weighed when assessing where to locate headwater linkage areas. Ideally, linkage areas will be located to provide the greatest benefit for species, while minimizing economic impacts from reduced commodity production. The following list might be considered during landscape planning when the location of linkage areas is discussed.

2.2.1. Known sites for headwater species of concern

Species knowledge can be used effectively to locate headwater linkage areas. For example, tailed frogs (*Ascaphus* spp.) and torrent salamanders (*Rhyacotriton* spp.) are species of concern in headwater streams of the Pacific Northwest that may use over-ridge corridors (Olson et al., 2007). Known locations of these species could be the basis for establishing headwater linkage areas. In the absence of site-specific knowledge of species occurrence, habitat models can predict areas of likely occurrence across a landscape. Several studies have addressed the site-level habitat associations of headwater amphibian species, with stream gradient, size, flow regime, and substrate composition being top predictors of occurrences (e.g., Russell et al., 2004; Dupuis and Steventon, 1999; Olson and Weaver, 2007; Welsh and Lind, 1996).

2.2.2. Existing protections for terrestrial species

Economy of space and resources argues that headwater linkage areas should overlap with existing protections. In our study area, these include habitat areas designated for general ecological integrity, notably late-successional reserves on federal lands (e.g., USDA and USDI, 1994), or for the benefit of particular species. Specifically, sites might be considered for linkage areas where terrestrial-obligate species are targeted, such as existing "owl cores" which are intended to protect nesting sites of the northern spotted owl (*Strix occidentalis caurina*). Such a provision could also protect rare or little known forest-dwelling taxa (Raphael and Molina, 2007), and locations of such rare taxa could be used with or without information on other headwater species or ecosystem processes. For example, priority sites are identified in the federal Conservation Strategy and Agreement to manage Oregon populations of the Siskiyou Mountains salamander (*Plethodon stormi*), a terrestrial-obligate salamander occurring in forested talus (Olson et al., 2009). Co-locating these upland salamander management areas across ridgelines of adjoining headwater drainages could provide the land–water connectivity in our proposed framework. Similarly, botanical set-asides are occasionally delineated in the Oregon Coast Range Province and could be considered during design of headwater links. Several legacy forest habitat elements might also be considered for co-location of linkage areas. Numerous taxa are associated with attributes of older forests, such as large trees and large dead wood (e.g., Johnson and O'Neil, 2001; Lindenmayer and Franklin, 2002). As these occur in headwaters or along ridgelines, they might become foci for linkage area placement. "Piggy-backing" protections for several purposes is a logical strategy in a forested landscape managed for multiple uses including timber harvest.

2.2.3. Short connections and paths of least resistance

Over-ridge linkage areas that minimize the slope-distance between wetted channels may be optimum for the numerous species with dispersal limitations or stream-riparian associations found in headwater drainages (Sheridan and Olson, 2003; Olson and Weaver, 2007; Olson et al., 2007; Wipfli and Gregovich, 2002; Sheridan and Spies, 2005). Of the three amphibian groups dominating headwater systems in the Pacific Northwest, *Ascaphus*, *Rhyacotriton*, and *Dicamptodon*, torrent salamanders may be most restricted in their overland movements. Nevertheless, individuals have been found 30–40 m from streams (Vesely, 1996) and in a pitfall trap 200 m from a stream (Gomez and Anthony, 1996). Tailed frogs and Pacific giant salamanders (*Dicamptodon* spp.) have been more frequently found in upslope areas, with pitfall-trap captures at 100–400 m from streams (Gomez and Anthony, 1996; McComb et al., 1993a,b; Wahbe et al., 2004). Using these distances as a gauge, it can be most effective to design over-ridge linkage areas with short slope-distance connections between wetted channels.

Another factor in this regard would be to follow paths of least resistance for organism dispersal (Noss et al., 1997). The likelihood of dispersal may depend on the energetics of moving, such that easier paths may be traversed more frequently. This might take topography or other site conditions into account. For example, assessment of potential headwater linkage areas may reveal ridgelines with lower gradient or lower elevation access (e.g., "saddles") that may be more easily traversed by ground-dwelling organisms. For organisms that have wind-dispersal stages, paths of least resistance might take into account wind directions during the likely seasons of dispersal.

2.2.4. Disturbance

Incorporation of the stand-to-landscape dynamics generated by the natural disturbance regime is a fundamental concept for ecosystem management approaches in the US Pacific Northwest (Cissel et al., 1998; Spies et al., 2006). Natural disturbances in our study area include sub-drainage scale landslides and debris flows, vegetation damage from wind or ice, and fire. Because all of these disturbances have some propensity for headwater areas or ridgelines, overlays of hazard models can be used when designing linkage area locations. To hedge uncertainties, co-locating headwater linkage areas both within and outside of disturbance-prone areas might be considered.

For example, debris flows are key disturbances in many mountainous regions that scour or bury stream channels but also contribute physical habitat heterogeneity by delivering large wood into and through headwater channels (Benda and Cundy, 1990; Montgomery, 1999; Gomi et al., 2002; Benda et al., 2003). Timberland management can alter debris-flow characteristics, including the frequency, magnitude, and synchronicity of events across a landscape, which may negatively affect stream-dwelling organisms. Thus, attempting to maintain or restore debris-flow characteristics and the sources of wood for debris-flow delivery to streams are commonly seen as desirable policy goals. Models have been developed for the Oregon Coast Range Province to identify probable debris-flow sources (e.g., Miller and Burnett, 2007) and traversal corridors (Miller and Burnett, 2008) and then applied to demonstrate policy designs for protecting source areas and headwater streams prone to initiating and transporting debris flows (Burnett and Miller, 2007) (Fig. 5). Efforts to locate linkage areas for amphibians and other headwater-associated species can take advantage of these outputs either to avoid debris-flow prone areas or extend such areas if these are used in modifying extant riparian management zones.

Anthropogenic disturbances are an additional consideration. Knowledge of where human activities including roads, mines, urban and agricultural development, and recreation sites are located can be used to avoid disturbances that may reduce the effectiveness of linkage areas designed to retain habitat and species.

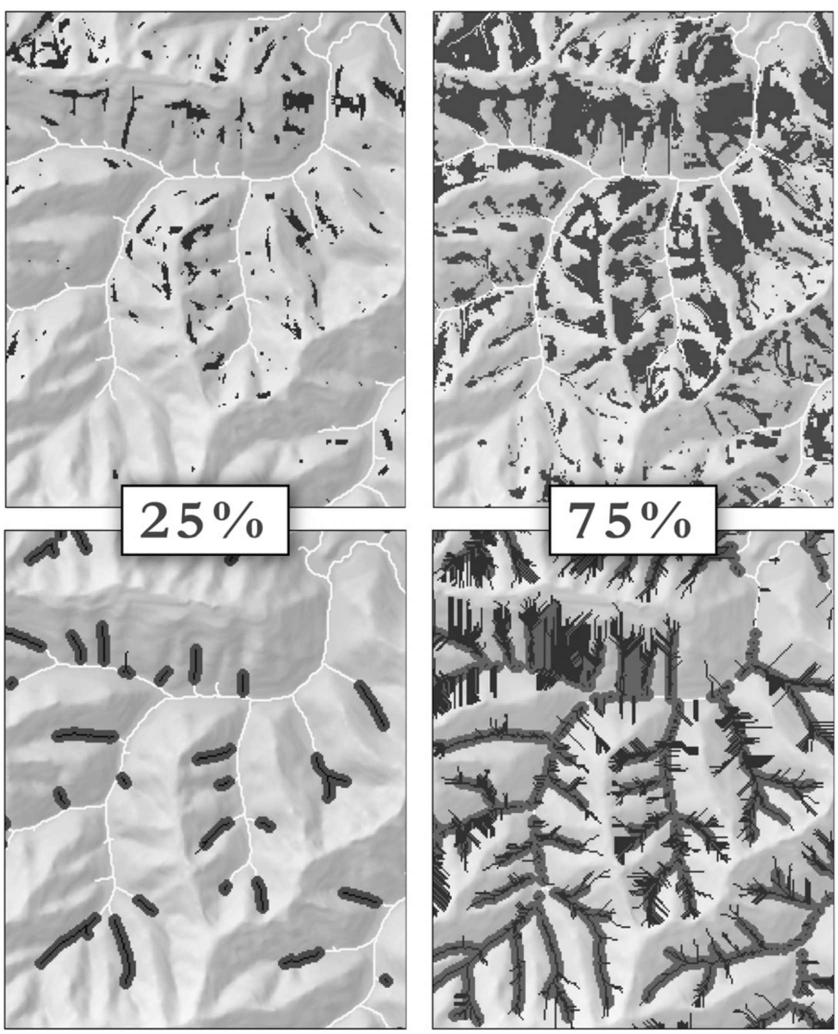

Fig. 5. Initiation and traversal zones for debris flows illustrated for the Knowles Creek basin, OR, USA that might be considered when designing headwater linkage areas at the basin scale. Top figures show results of a model identifying 25% and 75% of sites most prone to delivering landslides to a fish-bearing channel. Bottom figures show results of a model identifying 25% and 75% of the locations most likely to be traversed by debris flows that deliver to fish-bearing channels (Burnett and Miller, 2007). Gray polygons include 35-m buffers for traversal zones along all nonfish-bearing headwater streams. The modeled fish-bearing channel network is shown in white.

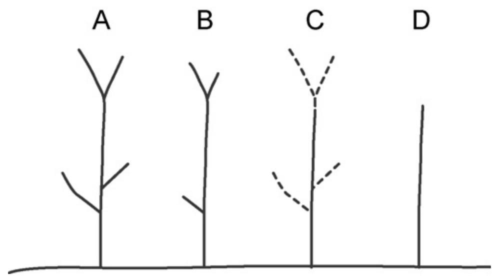

Fig. 6. Anticipated headwater stream flow changes with reduced precipitation, specifically for streams reliant on rain for surface flow. A–D show a progression of stream drying with reduced precipitation, from channels with varying perennial stream flow (solid lines) and spatially or temporally intermittent stream flow (dashed lines).

An emerging concern for habitats in headwater linkage areas is the potential effect of climate change. Scenarios of reduced or variable precipitation in our study area could affect habitats and species in headwater sub-drainages. Altered precipitation in forests could influence a variety of moisture-dependent species occurring in terrestrial microhabitats. For example, in eastern US forests, drought is implicated as a contributor to reduced survival due to desiccation of amphibians in upland areas (Rittenhouse et al., 2008, 2009). In a headwater stream context, reduced precipitation could shorten the length of wetted channels, particularly streams dependent upon rain or snow melt events for surface flow. Hence, "shrunken heads" may result with reduced precipitation (Fig. 6). Jefferson et al. (2008) provide preliminary support for reduced stream flow in some regions of western Oregon due to climate variation including warmer winters and earlier snowmelt. Interaction of climate variation with both species' responses and designation of headwater management strategies needs further development. However, the web of connectivity created by linkage areas over headwater ridgelines would likely aid species' dispersal and hedge uncertainty relative to this and numerous other disturbances not addressed here.

2.2.5. Land ownership and management direction

At the drainage-basin scale, but also at the larger landscape and smaller site scales of consideration, a politico-economic criterion for placement of linkage areas might include land ownership and associated land management practices. Areas along headwater streams on federal forest lands are designated as Riparian Reserves within the Oregon Coast Range province and active management is generally limited to that intended to benefit aquatic conservation (USDA and USDI, 1994). Extending these protections as linkage areas across ridgelines is a natural choice for maximizing contributions to biodiversity while minimizing constraints on timber harvest. As federal land ownerships occur in patches with intervening private lands, such as the "checkerboard" landscape of the US Bureau of Land management, then weighted retention of linkage areas to connect the federal patches might be considered, such as along diagonals of the federal checkerboard squares. In contrast, forest management on private lands in the Pacific Northwest is predominantly by clearcut harvest on relatively short rotations (e.g., 40 years) with few regulatory restrictions along headwater streams (see Olson et al., 2007). Linkage areas may be practical on such lands if a variety of mechanisms to bolster biodiversity conservation are explored, such as forest certification procedures (Suzuki and Olson, 2008).

2.3. Management alternatives for headwater linkage areas: forest-stand scale

A useful framework for designing stand-scale management approaches for headwater linkage areas may be to think of them as including "extenders" and "connectors," relative to existing riparian buffer networks. Extenders are additional riparian buffers that are delineated from buffered streams into non-buffered headwater streams, such as channels without fish on some land ownerships. These conceptually encompass the channel upslope of existing buffers, and may include crenulations, depressions, gullies or draws with perennial, intermittent or ephemeral surface flow, seepages, or wetlands. Connectors are the portion of a linkage area that is delineated from the uppermost channel over the ridgeline to a neighboring channel in the next drainage.

Widths of extenders and connectors could vary, depending upon site conditions, existing protections, considerations from larger spatial scales, and management directions on both sides of ridgelines. The effect of alternative riparian buffer widths with upland thinning is being examined in western Oregon in the federal Density Management Studies (Cissel et al., 2006), and those findings could be applied in this context (Fig. 7) (e.g., Olson and Rugger, 2007; Anderson et al., 2007; review in Olson et al., 2007). From the literature, several guidelines have emerged: (1) "wider is better" (Noss et al., 1997; Lindenmayer and Franklin, 2002); (2) the need to consider the spatial scale for which the linkage area will serve as a critical connection, with wider corridors for connections at larger spatial scales (Noss et al., 1997), for example, linkage areas connecting 4th-code HUs may need to be wider than those connecting 7th-code HUs within a single 6th-code HU; (3) it is important to evaluate consequences of edge effects, width–length ratios, and edge-to-interior ratios, for example relative to interior habitat suitability or potential increases in edge-associated predation (e.g., Noss et al., 1997); and (4) from a Brazilian study, corridor widths of 30–40 m were considered adequate for mammal migration, and 200-m widths were thought to be adequate for all species (Laurance and Laurance, 1999). To address uncertainties, a mix of widths for buffer extenders and over-ridge connectors might be considered.

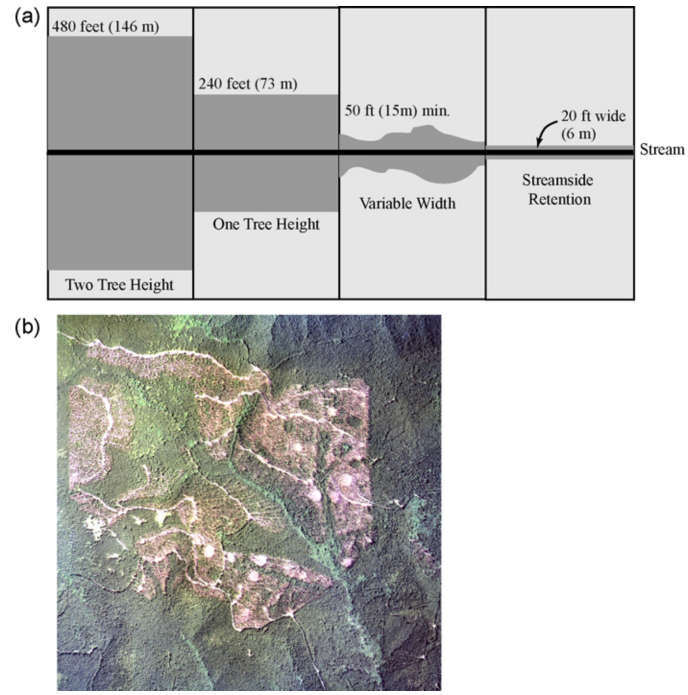

Fig. 7. Linkage areas between headwater drainages may consider extending riparian buffers of different widths across ridgelines or headwater-basin scale uncut blocks of forest. Treatment effects of buffers illustrated in (A) are shown as implemented in (B) for western Oregon, USA along with upland thinning (e.g., Olson and Rugger, 2007; Anderson et al., 2007) and deployment of leave islands and variable thinning densities (US Bureau of Land Management study site, OR, USA; Cissel et al., 2006).

Table 1
"Toolbox" of provisions to consider for within- and among-basin designs to provide habitat and linkage areas for aquatic-riparian dependent forest biodiversity such as amphibians and arthropods.

Provision	Implementation considerations	References
Riparian buffers	Vary widths to hedge effects "Soft" management within Extend to ridgelines as linkage areas Extend to uncut blocks of forest as linkage areas Position to manage for natural disturbance regime (link to landslide prone areas)	Olson et al. (2007), Olson and Rugger (2007), Rykken et al. (2007), Olson (2008a), Burnett and Miller (2007), Anderson et al. (2007) and Progar and Moldenke (2002)
Forest thinning	Variable densities to hedge effects Reduce ground disturbance during yarding	Kluber et al. (2008), Olson (2008b) and Wessell (2005)
Down wood	Retain and recruit	Olson et al. (2006), Kluber et al. (2009) and Rundio and Olson (2007)
Leave islands	Position in association with legacy features (large trees, large wood) Habitat diversity (seeps, talus) Biodiversity hotspots (deciduous trees) Sizes to retain interior conditions (e.g., >0.4 ha)	Neitlich and McCune (1997), Olson et al. (2007) and Wessell (2005)
Uncut blocks	To serve as habitat anchors Position at tributary junctions and headwater drainages	Olson et al. (2007)

Similarly, a mix of alternative silvicultural practices might be considered within extender or connector areas (Fig. 2), including variable density thinning with green-tree retention in clusters (leave islands). Leave island circles with areas of 0.4 ha retain interior microclimates (Wessell, 2005), and could provide refugia for some species closely associated with older-forest conditions. Leave islands might enhance biodiversity if located in conjunction with legacy forest features such as large trees, which can be biodiversity hotspots (Neitlich and McCune, 1997). Dead wood also may be a stand feature to retain and recruit in linkage areas for biodiversity maintenance (e.g., Rose et al., 2001; Olson et al., 2006; Rundio and Olson, 2007; Kluber et al., 2008, 2009). Microhabitat contiguity may be essential for dispersal-challenged canopy-dwellers such as lichens or red tree voles (*Arborimus longicaudus*), and hence retaining a string of contiguous vegetation may be a key consideration in some locations. If large, legacy trees exist along ridgelines, such strings may physically connect them to other trees along linkage areas. Hence overall, linkage areas may include unmanaged or managed forest stands. The toolbox of active stand-scale management approaches (Table 1) to retain forest biota and their habitats has been more fully discussed by Lindenmayer and Franklin (2002), McComb (2001) and Carey (2006). Management approaches for amphibians and reptiles in moist coniferous forests and riparian areas in northwestern North America are summarized in Olson (2008a,b).

3. Discussion

Biota in managed forest landscapes may be at risk due to habitat fragmentation affecting overland dispersal. In particular, a suite of species associated with headwater streams also uses the adjacent riparian and upslope forest habitats, and may be affected by some timber harvest practices and related activities, such as road building. To provide habitat connectivity over ridgelines for these and other forest-dependent species, we propose designation of headwater "linkage areas." We advance previous designs for headwater management areas (Olson et al., 2007; Cissel et al., 1998; Burnett and Miller, 2007) by considering implementation criteria for creating linkage areas extending riparian buffers over ridgelines to adjacent headwater riparian corridors to provide a web of relatively short-distance connections across large forest landscapes.

Our process of linkage area planning includes considerations at three spatial scales: landscape, drainage basin, and forest stand. At the largest scale, determining how many linkage areas may be needed across a forest landscape is a conceptual exercise to meld large scale forest patterns and processes with species life history parameters and population dynamics. The mid-scale and smaller stand-scale considerations would engage stakeholders managing lands across several drainage areas, and could result in a mix of strategies tuned to diverse land ownership priorities. Priority considerations for landscape-to-site integration of linkage area planning include: (1) use of 7th-code HUs for linkage area design across scales; (2) increasing linkage area density and widths with the spatial scale being connected, for example, linkages across 4th-code HU may be more frequent and/or wider than linkages across 7th-code HUs; (3) more linkage areas may be needed across north-south or altitudinal gradients to manage for effects of climate change; (4) linkage rates and locations may relate to intensities and frequencies of disturbances, such as landslides in headwater drainages; and (5) species knowledge of occupied habitats, habitat associations and dispersal behavior and capability, with linkage areas placed at shorter connections across paths of least resistance.

In the absence of species knowledge, an experimental approach might be initiated where drainages are identified to test alternative linkage designs. Mark-recapture or other species tracking methods can determine use of linkage areas relative to movements into surrounding managed "matrix" areas. We propose a 15% level of connectivity across the Coast Range Province of Oregon, for initial implementation and testing relative to headwater-associated amphibians. Genetic studies also may reveal past patterns of gene flow with environmental gradients, including parameters discussed here such as timber management (e.g., tailed frogs, Spear and Storfer, 2008), topography, and degree of aquatic connectivity. In the interim, the "more is better" guideline might be used to begin to construct a more-connected landscape, especially where species of concern are identified as management priorities and timber management activities predominate. Adaptive management is anticipated as new knowledge emerges relative to the interaction of species, ecological processes, and forest management practices.

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